

B R E V I O R A

Museum of Comparative Zoology



US ISSN 0006-9698

CAMBRIDGE, MASS.

17 JUNE 2015

NUMBER 546

MOVEMENT RATES OF THE LIZARD *ANOLIS CAROLINENSIS* (SQUAMATA: DACTYLOIDAE) IN THE PRESENCE AND ABSENCE OF *ANOLIS SAGREI* (SQUAMATA: DACTYLOIDAE)

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ABSTRACT. Shifts in a species' habitat can be precipitated by co-occurring with a closely related, ecologically similar species, to avoid negative interspecific interactions. Such shifts in habitat may also cause a change in movement behavior in sympatric populations compared with allopatric populations. *Anolis carolinensis* lizards are known to shift their habitat to higher perches in the presence of *Anolis sagrei*, and we examine whether movement rates differ between populations of *A. carolinensis* that are allopatric and sympatric with recently arrived *A. sagrei*. We find an interaction between the effects of sex and the presence of *A. sagrei* on movement rates, indicating that males and females respond differently in their movement rates to the presence of a congener. We suggest that variation in the motivation for movement between the sexes may explain intraspecific relationships between movement and habitat.

KEY WORDS: foraging; Florida; spoil islands; invasive species

INTRODUCTION

Habitat use can differ among populations of a species that are either sympatric or allopatric with closely related, ecologically similar species (e.g. Schoener, 1975; Medel *et al.*, 1988; Schluter and McPhail, 1992;

Dietrich and Werner, 2003). Interspecific interactions often have negative fitness consequences (Polis *et al.*, 1989; Gronig and Hochkirch, 2008; Grether *et al.*, 2009; Hendry *et al.*, 2009), and shifts in the habitat used by one or both species when they co-occur can reduce the frequency of such interactions.

Although sympatric habitat shifts themselves have been frequently documented (Schluter, 2000; Stuart and Losos, 2013), the behavioral consequences of such shifts are not well studied. One behavior, movement, is important to organisms for a variety of reasons, including foraging, territory defense,

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intersexual interactions, and escape from predators (Losos, 1990; Jayne and Irschick, 2000; Anderson, 2007; Huey and Pianka, 2007). Movement behavior can be influenced by the habitat in which individuals occur. For example, individuals occupying habitats that differ in prey type, location, and density (e.g., Bottom and Jones, 1990; Ives *et al.*, 1993) may vary in the number of movements made while foraging (Eifler and Eifler, 1999; Greef and Whiting, 2000; Barahona and Navarrete, 2009). The ecological consequences of variation in movement rates are also diverse and may include effects on foraging success, predation risk, and energy expenditure. Nevertheless, to our knowledge, only a few studies have shown that changes in habitat use can result in altered movement rates within species (e.g., Barahona and Navarrete, 2009; Hovel and Wahle, 2010).

Anolis lizards offer an excellent opportunity for studying the effects of intraspecific variation in habitat use on movement rates. These arboreal, insectivorous lizards are known to vary in habitat use between sympatric and allopatric populations; in many *Anolis* species, the average perch height of individuals in populations sympatric with other anoles differs from the average perch height of individuals in allopatric populations (Jenssen, 1973; Schoener, 1975; Jenssen *et al.*, 1984; Losos *et al.*, 1993; Losos and Spiller, 1999; Kolbe *et al.*, 2008; Stuart *et al.*, 2014). Moreover, both interspecific and intraspecific variation in movement rates in anoles suggest that movement rates are related to habitat. In the Greater Antilles, *Anolis* lizards have repeatedly evolved to specialize on particular microhabitats within the arboreal habitat, and anole species that perch low on tree trunks (trunk-ground ecomorphs) have lower movement rates than lizards perching higher on tree trunks and in the canopy (trunk and trunk-crown ecomorphs; Cooper, 2005; Johnson *et al.*, 2008). Within

species, however, the relationship between movement rates and perch height differs among different microhabitat specialists (Cooper, 2005) and may co-vary with changes in season (Lister and Aguayo, 1992; Jenssen *et al.*, 1995). In general, the ecological forces shaping the associations between habitat and movement rates remain unknown (Johnson *et al.*, 2008). In particular, we do not know whether a habitat shift due to the presence of a congener can affect movement rates.

Almost all previous research on movement rates in anoles has been conducted on males (Moermond, 1979; Cooper, 2005; Johnson *et al.*, 2008); indeed, research on female anoles has often lagged behind research on male anoles (Butler *et al.*, 2007; Losos, 2009). Male and female lizards spend a majority of their time engaged in different activities during the breeding season (Jenssen *et al.*, 1995; Nunez *et al.*, 1997), but we do not know if this difference causes males and females to move at different rates or if the presence of a congener can affect male and female movement behavior in different ways.

In the southeastern United States, the native *Anolis carolinensis* co-occurs widely with the invasive *Anolis sagrei*, and these two ecologically similar species interact strongly with one another. Closely related and morphologically similar to high-perching trunk-crown anoles in Cuba (Williams, 1969; Glor *et al.*, 2005; Campbell-Staton *et al.*, 2012), *A. carolinensis* perches at low heights in the absence of other *Anolis* lizards but shifts to higher perches in the presence of the larger, also low-perching *A. sagrei* (Collette, 1961; Edwards and Lailvaux, 2012; Stuart *et al.*, 2014). In this study, we assess the effect of the presence of *A. sagrei* on the movement rates of male and female *A. carolinensis* by comparing populations of *A. carolinensis* where they are the only anoles present to populations of *A. carolinensis* where they co-occur with *A. sagrei*.

METHODS

This study was carried out from June to August 2010 in Mosquito Lagoon, Florida, on small dredge-spoil islands that are home to either only *A. carolinensis* (one-species islands) or both *A. carolinensis* and *A. sagrei* (two-species islands). Three one-species islands (Crescent, Hornet, South Twin) and two two-species islands (Line of Cedars, Lizard) were sampled here. One- and two-species islands did not differ in geographic or environmental characteristics apart from the presence of *A. sagrei* (Kamath *et al.*, 2013; Stuart *et al.*, 2014). Therefore, differences in *A. carolinensis* behavior between one- and two-species islands are most likely attributable to the presence of *A. sagrei* rather than to environmental differences among islands with and without *A. sagrei*. Previous research has confirmed that both male and female *A. carolinensis* move to higher perches on two-species islands compared with one-species islands in Mosquito Lagoon (Campbell, 2000; Stuart *et al.*, 2014).

Focal observations lasting up to 20 minutes or until the lizard disappeared from view were conducted on undisturbed male and female lizards between 0700 and 1700 hours from 22 June to 6 August, 2010. A single observer (AK) watched individual lizards through binoculars, noting the number of movements made by the lizard in the time observed. Observations were only conducted in relatively open habitats, to ensure that a distance of at least 2 m was maintained between the lizard and the observer. If possible, lizards were caught and temporarily marked with a Sharpie® marker after the observation period to ensure that lizards were not re-sampled during subsequent visits.

For each lizard, we calculated the number of movements per minute (MPM), a movement rate index often used for lizards, including anoles (Cooper, 2005; Johnson

et al., 2008). Observations that lasted less than five minutes or observations where $MPM < 0.25$ were excluded from subsequent analyses to exclude lizards potentially disturbed by the observer's presence (following Johnson *et al.*, 2008; mean length [\pm standard deviation] of observations included: 15.6 ± 5.1 minutes). We square root-transformed MPM before statistical analysis to improve the normality of model residuals. We compared MPM for males and females between island types using a linear mixed effects model in R (*nlme* package; Pinheiro *et al.*, 2013) with *A. sagrei* presence and sex as fixed effects, the interaction term *A. sagrei* presence \times sex, and a random effect of island. Next, we split the data set by *A. carolinensis* sex and used a mixed effects model with a fixed effect of *A. sagrei* presence and a random effect of island to assess the effect of *A. sagrei* presence on MPM for males and females separately. Statistical significance was assessed by comparison with a null model in which the term of interest was dropped, using a likelihood ratio test. Statistical analyses were conducted in R version 3.0.2 (R Core Team, 2013).

RESULTS

A total of 204 *A. carolinensis* individuals were observed for this study, including 42 females and 68 males from one-species islands and 36 females and 58 males from two-species islands. Across all observations with $MPM > 0.25$, the mean and standard deviation of MPM was 1.29 ± 0.75 , which is comparable in magnitude to previous estimates of movement rates of trunk-crown anoles (Johnson *et al.*, 2008). Movement rates varied substantially across individual observations, with coefficients of variation of MPM within islands ranging from 41% to 74%; the coefficient of variation of island means of MPM was 25%.

A significant interaction between *A. sagrei* presence and *A. carolinensis* sex on MPM ($\chi^2_{(1)} = 7.11$, $P = 0.007$; Fig. 1) suggests that the sexes differ in how MPM varies with the presence of *A. sagrei*. Upon splitting the dataset by *A. carolinensis* sex, we found that males have lower MPM on two-species islands than on one-species islands ($\chi^2_{(1)} = 6.58$, $P = 0.01$), whereas MPM does not differ between females on one- and two-species islands ($\chi^2_{(1)} = 1.39$, $P = 0.24$; Fig. 1).

DISCUSSION

Despite substantial variation among individuals and across islands in movement rates, we found an interaction between the effect of *A. sagrei* and the sex of *A. carolinensis* on MPM, suggesting that movement rates in male and female *A. carolinensis* are affected differently following a shift to higher perches in the presence of *A. sagrei*. In particular, male *A. carolinensis* move less often in the presence of *A. sagrei*, whereas the movement rates of female *A. carolinensis* are unchanged in the presence of *A. sagrei*.

That males and females differ behaviorally in their response to *A. sagrei* is not surprising, because males and females have different



Figure 1. Movements per minute (MPM) of male and female *Anolis carolinensis* on one- and two-species islands (i.e., in the absence and presence of *Anolis sagrei*). Points represent the mean of island means for males (closed squares) and females (open circles) on each type of island, with error bars showing the standard deviation in island means.

motives for movement during the breeding season. Male anoles, including *A. carolinensis*, spend a majority of their time in the breeding season engaged in social interactions (Andrews, 1971; Fleming and Hooker, 1975; Lister and Aguayo, 1992; Jenssen *et al.*, 1995). Females, on the other hand, spend most of their time foraging in both the breeding and the non-breeding seasons (Lister and Aguayo, 1992; Nunez *et al.*, 1997). This difference between the sexes in their reasons for moving suggests that even though MPM is usually considered an index of foraging behavior for lizards, it is better interpreted in a context-specific manner (Perry, 2007; Reilly *et al.*, 2007). In studies conducted during the breeding season, such as this one, MPM should be interpreted as an index of sit-and-wait foraging vs. active foraging only for females. The absence of a change in MPM in sympatric females relative to allopatric females suggests that lizards do not forage more actively in the presence of *A. sagrei*, despite shifting to higher perches. Nevertheless, it seems unlikely that females move solely to forage (Nunez *et al.*, 1997). Although it will always be challenging to determine the motivation for a given individual's movement, repeated observations of individuals in different seasons, at different times of day, and in different social and ecological contexts might lend further insight into variation in movement rates of lizards.

In contrast to females, male *A. carolinensis* move less often in the presence than in the absence of *A. sagrei*. Decreased movement rates in anoles can be related to increased perch height, as has been documented in males in the trunk-crown anole *Anolis stratulus* as well as several grass-bush anoles (Cooper, 2005). The shift of male *A. carolinensis* to higher perches in the presence of *A. sagrei* (Stuart *et al.*, 2014) may thus drive the decrease in movement rates in male *A.*

carolinensis observed here. Although changes in habitat visibility with perch height have long been considered to underlie these relationships (Moermond, 1979; Cooper, 2005), the precise mechanisms that lead movement rate and habitat to be associated with one another remain unknown, and the opposite relationship between perch height and movement rates has also been observed previously (Johnson *et al.*, 2008). Such contradictions can be seen within our data set as well—females, who tend to perch lower than males (Schoener, 1968; Perry, 1996), have a lower movement rate than males on one-species islands (Fig. 1).

Male anoles spend a majority of their time in the breeding season engaged in social interactions and territory defense (Andrews, 1971; Fleming and Hooker, 1975; Lister and Aguayo, 1992; Jenssen *et al.*, 1995), and decreased movement rates in male *A. carolinensis* on two-species islands might result from changes in territory size and social interactions due to the presence of *A. sagrei*. Territory size decreases with increasing lizard density in anoles (Schoener and Schoener, 1982), and *A. sagrei* reaches high densities on small islands even in the presence of other anoles (Losos and Spiller, 1999, Campbell and Echternacht, 2003). If male *A. sagrei* and *A. carolinensis* territories do not overlap to avoid interspecific interactions, *A. carolinensis* territories may be smaller on two-species islands due to the increased combined population density of *A. carolinensis* and *A. sagrei* on two-species islands. Territory size may also decrease at higher perches due to reduced visibility in the canopy because of the challenges of preventing intruders from entering a large territory in a visually cluttered environment (Eason and Stamps, 1992). Sympatric males might therefore require fewer movements to defend these potentially smaller territories than allopatric males. Alternatively, because the population densities of *A. carolinensis* decrease in the

presence of *A. sagrei* (Campbell, 2000), male *A. carolinensis* on two-species islands might encounter fewer conspecific male rivals and may therefore need to move less often to display to conspecifics and defend their territories against intruders.

Much more attention has been paid to the behavioral ecology of male anoles than to that of female anoles (Butler *et al.*, 2007; Losos, 2009). Our results suggest that male and female anoles can differ in their behavioral responses to ecological pressures. Understanding the mechanisms leading to behavioral and ecological variation within a species will therefore depend upon documenting this variation in both males and females, a conclusion that is hardly surprising. It is disappointing that research on fundamental aspects of the biology of even organisms as well-studied as *Anolis* lizards remains largely focused on males.

Although we do not know the mechanisms driving changes in movement behavior, our study indicates that novel interaction with a congeneric competitor has further behavioral consequences for *A. carolinensis* individuals beyond a shift in habitat. However, some behaviors of *A. carolinensis*, such as the partitioning of feeding and displaying into different microhabitats, remain unchanged in the presence of *A. sagrei* (Kamath *et al.*, 2013). The behavioral consequences of strong ecological interactions are therefore complex and not easily predicted, and intensive observations of individuals in the field will be central to fully understanding how co-occurring with an ecologically similar congener can shape intraspecific variation in behavior.

ACKNOWLEDGMENTS

We thank Mike Legare and James Lyon at Merritt Island National Wildlife Refuge (U.S. Fish and Wildlife Service) and John Stiner and Candace Carter at Canaveral

National Seashore (U.S. National Park Service) for their gracious help with permits and logistics. Jim McRae generously lent us his boat to access the islands. We thank Jonathan Losos and two anonymous reviewers for comments that improved the manuscript. AK was supported by the Amherst College Schupf Scholars Program and YES by a Museum of Comparative Zoology Miyata Award.

LITERATURE CITED

- ANDERSON, R. A. 2007. Food acquisition modes and habitat use in lizards: questions from an integrative perspective, pp. 450–490. In S. M. Reilly, L. B. McBrayer, and D. B. Miles (eds.). *Lizard Ecology*. Cambridge, U.K., Cambridge University Press.
- ANDREWS, R. M. 1971. Structural habitat and time budget of a tropical *Anolis* lizard. *Ecology* **52**: 262–270.
- BARAHONA, M., AND S. A. NAVARRETE. 2009. Movement patterns of the seastar *Heliaster helianthus* in central Chile: relationship with environmental conditions and prey availability. *Marine Biology* **157**: 647–661.
- BOTTOM, D. L., AND K. K. JONES. 1990. Species composition, distribution and invertebrate prey of fish assemblages in the Columbia River estuary. *Progress in Oceanography* **25**: 243–270.
- BUTLER, M. A., S. A. SAWYER, AND J. B. LOSOS. 2007. Sexual dimorphism and adaptive radiation in *Anolis* lizards. *Nature* **447**: 202–205.
- CAMPBELL, T. S. 2000. Analyses of the effects of an exotic lizard (*Anolis sagrei*) on a native lizard (*Anolis carolinensis*) in Florida, using islands as experimental units. Unpublished Ph.D. Thesis. Knoxville, University of Tennessee.
- CAMPBELL, T. S., AND A. C. ECHTERNACHT. 2003. Introduced species and moving targets: changes in body sizes of introduced lizards following experimental introductions and historical invasions. *Biological Invasions* **5**: 193–212.
- CAMPBELL-STATON, S. C., R. M. GOODMAN, N. BACKSTRÖM, S. V. EDWARDS, J. B. LOSOS, AND J. J. KOLBE. 2012. Out of Florida: mtDNA reveals patterns of migration and Pleistocene range expansion of the green anole lizard (*Anolis carolinensis*). *Ecology and Evolution* **2**: 2274–2284.
- COLLETTE, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bulletin of the Museum of Comparative Zoology* **125**: 137–162.
- COOPER, W. E. 2005. Ecomorphological variation in foraging behaviour by Puerto Rican *Anolis* lizards. *Journal of Zoology* **265**: 133–139.
- DIETRICH, B., AND R. WERNER. 2003. Sympatry and allopatry in two desert ant sister species: how do *Cataglyphis bicolor* and *C. savignyi* coexist? *Oecologia* **136**: 63–72.
- EASON, P. K., AND J. A. STAMPS. 1992. The effect of visibility on territory size and shape. *Behavioral Ecology* **3**: 166–172.
- EDWARDS, J. R., AND S. P. LAILVAUX. 2012. Display behavior and habitat use in single and mixed populations of *Anolis carolinensis* and *Anolis sagrei* lizards. *Ethology* **118**: 494–502.
- EIFLER, D. A., AND M. A. EIFLER. 1999. The influence of prey distribution on the foraging strategy of the lizard *Oligosoma grande* (Reptilia: Scincidae). *Behavioral Ecology and Sociobiology* **45**: 397–402.
- FLEMING, T. H., AND R. S. HOOKER. 1975. *Anolis cupreus*: the response of a lizard to tropical seasonality. *Ecology* **56**: 1243–1261.
- GLOR, R. E., A. LARSON, AND J. B. LOSOS. 2005. Out of Cuba: overwater dispersal and speciation among lizards in the *Anolis carolinensis* subgroup. *Molecular Ecology* **14**: 2419–2432.
- GREEF, J.M., AND M. J. WHITING. 2000. Foraging-mode plasticity in the lizard *Platysaurus broadleyi*. *Herpetologica* **56**: 402–407.
- GREYER, G. F., N. LOSIN, C. N. ANDERSON, AND K. OKAMOTO. 2009. The role of interspecific interference competition in character displacement and the evolution of competitor recognition. *Biological Reviews* **84**: 617–635.
- GRONIG, J., AND A. HOCHKIRK. 2008. Reproductive interference between species. *The Quarterly Review of Biology* **83**: 257–282.
- HENDRY, A. P., S. K. HUBER, L. F. DE LEÓN, A. HERREL, AND J. PODOS. 2009. Disruptive selection in a bimodal population of Darwin's finches. *Proceedings of the Royal Society B* **276**: 753–759.
- HOVEL, K. A., AND R. A. WAHLE. 2010. Effects of habitat patchiness on American lobster movement across a gradient of predation risk and shelter competition. *Ecology* **91**: 1993–2002.
- HUEY, R. B., AND E. R. PIANKA. 2007. Historical introduction: on widely foraging for Kalahari lizards, pp. 1–10. In S. M. Reilly, L. B. McBrayer, and D. B. Miles (eds.). *Lizard Ecology*. Cambridge, U.K., Cambridge University Press.
- IVES, A. R., P. KAREIVA, AND R. PERRY. 1993. Response of a predator to variation in prey density at 3 hierarchical scales – lady beetles feeding on aphids. *Ecology* **74**: 1929–1938.

- JAYNE, B. C., AND D. J. IRSCHICK. 2000. A field study of incline use and preferred speeds for the locomotion of lizards. *Ecology* **81**: 2969–2983.
- JENSSEN, T. A. 1973. Shift in the structural habitat of *Anolis opalinus* due to congeneric competition. *Ecology* **54**: 863–869.
- JENSSEN, T. A., D. L. MARCELLINI, C. A. PAGUE, AND L. A. JENSSEN. 1984. Competitive interference between the Puerto Rican lizards, *Anolis cooki* and *A. cristatellus*. *Copeia* **1984**: 853–862.
- JENSSEN, T. A., N. GREENBERG, AND K. A. HOVDE. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetological Monographs* **9**: 41–62.
- JOHNSON, M. A., M. LEAL, L. R. SCHETTINO, A. C. LARA, L. J. REVELL, AND J. B. LOSOS. 2008. A phylogenetic perspective on foraging mode evolution and habitat use in West Indian *Anolis* lizards. *Animal Behaviour* **75**: 555–563.
- KAMATH, A., Y. E. STUART, AND T. S. CAMPBELL. 2013. Behavioral partitioning by the native lizard *Anolis carolinensis* in the presence and absence of the invasive *Anolis sagrei* in Florida. *Breviora* **535**: 1–10.
- KOLBE, J. J., P. L. COLBERT, AND B. E. SMITH. 2008. Niche relationships and interspecific interactions in Antiguan lizard communities. *Copeia* **2008**: 261–272.
- LISTER, B. C., AND A. G. AGUAYO. 1992. Seasonality, predation, and the behaviour of a tropical mainland anole. *Journal of Animal Ecology* **61**: 717–733.
- LOSOS, J. B. 1990. Concordant evolution of locomotor behaviour, display rate, and morphology in *Anolis* lizards. *Animal Behaviour* **39**: 879–890.
- LOSOS, J. B. 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. Berkeley, University of California Press.
- LOSOS, J. B., J. C. MARKS, AND T. W. SCHOENER. 1993. Habitat use and ecological interactions of an introduced and a native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes of anole introductions. *Oecologia* **95**: 525–532.
- LOSOS, J. B., AND D. A. SPILLER. 1999. Differential colonization success and asymmetrical interactions between two lizard species. *Ecology* **80**: 252–258.
- MEDEL, R. G., P. A. MARQUET, AND F. M. JAKSIC. 1988. Microhabitat shifts of lizards under different contexts of sympatry: a case study with South American *Liolaemus*. *Oecologia* **76**: 567–569.
- MOERMOND, T.C. 1979. The influence of habitat structure on *Anolis* foraging behavior. *Behaviour* **70**: 147–167.
- NUNEZ, S. C., T. A. JENSSEN, AND K. ERSLAND. 1997. Female activity profile of a polygynous lizard (*Anolis carolinensis*): Evidence of intersexual asymmetry. *Behaviour* **134**: 205–223.
- PERRY, G. 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behaviour and diet. *Canadian Journal of Zoology* **74**: 1238–1425.
- PERRY, G. 2007. Movement patterns in lizards: measurement, modality, and behavioral correlates, pp. 13–48. In S. M. Reilly, L. B. McBrayer, and D. B. Miles (eds.). *Lizard Ecology*. Cambridge, U.K., Cambridge University Press.
- PINHEIRO, J., D. BATES, S. DEBROY, D. SARKAR, AND THE R DEVELOPMENT CORE TEAM. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1 1-113.
- POLIS, G. A., C. A. MYERS, AND R. D. HOLT. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**: 297–330.
- R CORE TEAM. 2013. R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.
- REILLY, S. M., L. B. MCBRAYER, AND D. B. MILES (eds.). 2007. *Lizard Ecology*. Cambridge, U.K., Cambridge University Press.
- SCHLUTER, D. 2000. *The Ecology of Adaptive Radiation*. New York, Oxford University Press.
- SCHLUTER, D., AND J. D. MCPHAIL. 1992. Ecological character displacement and speciation in sticklebacks. *American Naturalist* **140**: 85–108.
- SCHOENER, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**: 704–726.
- SCHOENER, T. W. 1975. Presence and absence of habitat shift in some widespread lizard species. *Ecological Monographs* **45**: 233–258.
- SCHOENER, T. W., AND A. SCHOENER. 1982. Intraspecific variation in home-range size in some *Anolis* lizards. *Ecology* **63**: 809–823.
- STUART, Y. E., T. S. CAMPBELL, P. A. HOHENLOHE, R. G. REYNOLDS, L. J. REVELL, AND J. B. LOSOS. 2014. Rapid evolution of a native species following invasion by a congener. *Science* **346**: 463–466.
- STUART, Y. E., AND J. B. LOSOS. 2013. Ecological character displacement: glass half full or half empty? *Trends in Ecology and Evolution* **28**: 402–408.
- WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *The Quarterly Review of Biology* **44**: 345–389.